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# Developing a Carbon Budget, Physiology, Growth and Yield Potential Model for Almond Trees

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**Project No.:** 14-PREC1-DeJong

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**Objectives:**

This project had two objectives. The main objective was to develop a comprehensive functional-structural tree model of almond tree architectural development and growth, carbon partitioning/source-sink interactions, annual and multi-year carbon budgets and yield potential of almond trees. This model simulates growth and physiological responses to light distribution within an almond tree canopy as well as daily temperature and water potential changes over multiple years. It can also simulate growth responses to user-guided pruning practices.

A second objective was to complete collection of data on almond tree growth, standing orchard biomass and orchard productivity. The data generated in this objective are useful for estimating the amount of carbon sequestered in the standing biomass of almond orchards as well as providing data for validating the long-term biomass accumulation projections of the L-Almond model that was developed in the main objective.

## **Interpretive Summary:**

Objective one: Almond tree growth and yield is dependent on a complex set of interactions involving the plant genotype, the physiological and developmental processes that occur within the tree, the interaction of these processes with the environment that the tree grows in, and responses to horticultural manipulation of the tree by a grower. Understanding carbon budget, growth and yield responses of perennial crops like almond are even more complex than most crops because the effects of all these factors are carried out over multiple years.

Recent advances in computer technology have made it possible to develop functional-structural plant models that simultaneously simulate whole plant photosynthesis, tree architectural growth and carbon partitioning within the structure of the tree, and to display tree structural development in three dimensions on a computer screen. The most advanced of these types of models is the L-Peach model (Allen et al. 2005, 2007; Lopez et al. 2008). One objective of this project was to convert the L-Peach model to an L-Almond model.

The first step for conversion of L-Peach to an L-Almond model was to develop statistical models to describe patterns of buds that occur along Nonpareil almond shoots of different lengths. Development of these statistical shoot bud fate models for Nonpareil has been completed. The second step was to begin converting the L-Peach model into an L-Almond model by inserting leaf photosynthetic characteristics of almond trees and the statistical models of almond shoots into the L-Peach model. The third step was to incorporate a new canopy light distribution program into the model and also develop a new sub-model for the shedding of leaves and stems that are located in the excessively shaded areas of the canopies. This was necessary because almond trees are not pruned as hard as peach trees.

The initial development of the L-Almond model is complete and we can successfully simulate the architectural growth and yield of Nonpareil almond trees into the 5<sup>th</sup> year of growth in an orchard.

Objective two: For the past several years we have been working with an orchard removal company to obtain data on the amount of biomass removed from sites where orchards have been removed. Since tree size and density vary greatly among orchards we began to test a simple method for estimating standing biomass of existing orchards by surveying specific orchards prior to removal to determine the average tree trunk cross sectional area (TCSA) per acre. We then developed a mathematical relationship between TCSA/acre and the amount of biomass removed in the clearing process. Preliminary data showed that survey measurements of trunk cross sectional area were useful when the orchards being removed were mainly intact (few missing trees), but of more limited use in old orchards with many missing trees or trees of non-uniform age. Consequently, we began testing whether orchard standing biomass can be estimated more easily from detailed analysis of aerial images of orchards available from Google-

earth images. This work is nearly complete and we are in the process of writing the results up for publication.

Corollary efforts associated with this project have been the analysis of data from Regional Variety Trials and the spur dynamics study carried out by Dr. Lampinen's laboratory from 2001 to 2007, in order to develop data on long-term spur behaviour that could inform development and testing of the L-Almond model. Research by a PhD student not directly involved with this project but associated with Dr. DeJong's laboratory has also provided valuable insights into the chilling requirements of almond trees that will be valuable for eventually modelling tree growth and yield of almond trees over multiple years. Collectively the research associated with this project has provided valuable insights into the fruit production behaviour of almond trees that are useful for general understanding of almond tree productive behaviour as well as for developing the L-Almond model.

## **Materials and Methods:**

### **Development of an L-Almond Model**

Developing a model of almond tree growth began with statistically analyzing the structural patterns of various sizes of almond shoots using Hidden Semi-Markov Chain (HSMC) analysis techniques (Guedon et al. 2001). This work began in 2010 in a commercial 4-year-old almond orchard located near Sutter. This orchard had three cultivars ('Nonpareil', 'Aldrich', and 'Winters') exhibiting different tree architectures. Trees in the orchard were minimally pruned after the first year after planting, when the main scaffolds were chosen, so that trees developed their own architecture. Details of this study are presented in Negron et al. 2013. Two additional studies of almond shoot architectural structure were completed. One investigated the influence of water stress on shoot architecture (Negron et al. 2014) and another investigated the effects of pruning severity on subsequent shoot structure (Negron et al. 2015)

Shoot structural models from these studies were inserted into the L-Almond model in the same way as previously done for the L-Peach simulation model (Smith et al. 2008). Previously collected data on almond leaf and fruit growth characteristics (Esparza et al. 1999) were also used to convert the photosynthesis and fruit growth sections of the latest versions of the L-Peach model (Da Silva 2011 and 2014) into an L-Almond model.

When the initial L-Almond model was run with the updated shoot Markov-chain models, the model crashed in the 3<sup>rd</sup> or 4<sup>th</sup> year of simulated runs due to excessive canopy complexity. This was due to an inadequate within-canopy light simulation model and the related inability to program leaf and shoot death based on simulated internal canopy shading. An L-systems computer programming expert from the Computer Science Department at the University of Calgary (Dr. Mik Cieslak) was engaged on a short-term contract to address this issue with new canopy light simulation and stem shedding sub-models. Subsequently a new version of the L-Almond model with shadow propagation and leaf/stem shedding sub-models was developed and tested.

### **Assembling Data on Whole Tree Biomass**

We have developed a working relationship with G & F Agricultural Services Inc. and have cooperated with them to compile data on recently removed orchards. While we were doing this data compilation, we realized that we needed to develop a surveying method that would allow us to relate biomass removal data with average tree size prior to tree removal. Since tree trunk cross sectional area (TCSA) is a common method to estimate tree size used in horticulture as well as forestry, we tested a linear plot sampling method to quickly determine the mean TCSA/acre of specific orchards slated for removal, prior to their actual removal. This method allowed good biomass estimations for intact orchards but was not adequate for orchards with numerous missing trees or a wide range of trees sizes. To address this, we accessed Google-earth images of orchards prior to their removal to correct previously surveyed orchards for missing trees. These images provided additional information to improve our original estimations of orchard standing biomass using trunk cross sectional area orchard surveys.

### **Associated Studies**

A corollary effort associated with this project has been the analysis of data from the Regional Variety trials sponsored by the Almond Board (1993-2005) and from the spur dynamics study carried out by Dr. Lampinen's laboratory from 2001 to 2007. This was done to develop an understanding of factors controlling bearing and long-term spur behaviour needed for developing and validating the L-Almond model. We published research papers from this effort in 2010, 2011 and 2015. We have submitted one additional paper from these studies that indicates that almond tree yields are more related to the abundance of flowers than the percent of flowers that set fruit in well-managed orchards with adequate pollinators.

### **Results and Discussion:**

#### **Development of the L-Almond Model**

The L-Peach model has been successfully converted to an L-Almond model. Physiological functions describing the behavior of almond fruits and leaves needed to make this conversion came mainly from the DeJong laboratory (Grossman and DeJong 1994, Esparza et al 1999, Esparza et al 2001a). Statistical shoot models for describing the architecture and bud fates of Nonpareil shoots were developed (Negron et al. 2013) and inserted into the simulation model.

With the addition of the shadow propagation and leaf/stem shedding sub-models the new L-ALMOND model did a reasonable job of simulating the architectural tree growth, seasonal patterns of accumulated photosynthesis and respiration, accumulation of stem segments (internodes) and their dry weight as well as annual patterns of tree productivity (**Figures 1 - 5**). The total accumulated stem biomass in carbohydrate equivalents of a little over 300 kilograms per simulated tree growing without water or nutrient stress or shading from neighboring trees was very similar to the total harvested biomass of 8-year-old Nonpareil almond trees growing under field conditions in the

southern San Joaquin Valley of California (Esparza et al. 2001a). The fruit yields of approximately 25 kg/tree of the simulated 5-year-old trees was substantially lower than those attained for 7-yr-old field grown Nonpareil almond trees (approximately 40 kg/tree; Esparza et al 2001b) but this would be expected since almond tree yields typically increase significantly each year up to the age of 9 to 11 years (Duncan and Lampinen 2014). The number of fruit set per tree in the 5th simulated growing season (~5500) was only slightly higher than reported for 5th year almond trees growing in an orchard in northern California (4783 nuts/tree; Negron 2012).

The influence of the shadow propagation sub-model for simulating the effects of excess shade can be clearly seen by comparing the lower parts of the simulated June canopies in the 4th and 5th year trees (**Figure 2**). The bare zone in the lower part of the 5-year-old trees was a result of simulated shoot and spur abortion caused by excess shading. This is a fairly common phenomenon in field grown trees however the response of the model appears a little exaggerated. This is partially because the current model does not accommodate limb bending as a consequence of crop loads which naturally tends to “open up the tree” and let more light into the lower part of the canopy. Incorporating limb bending in response to crop load such as done for apricots by Almeras et al. (2002) would undoubtedly make simulations more realistic but would also significantly increase calculation times which are already a major issue with the current version of the L-Almond model. Nevertheless, we have successfully created a working version of the L-Almond model that appears to function satisfactorily. This model is the most advanced computer simulation model of nut tree development, growth and physiology currently in existence.

In the process of developing this model we became increasingly aware of the importance of overwintering carbohydrate storage and mobilization in the permanent structures of trees and the general lack of detailed knowledge about this aspect of tree physiology. The modeling work as well as the spur dynamics research pointed out the critical importance of springtime mobilization and transport of stored carbohydrates for supplying the needs of rapidly expanding flowers, young fruit, leaves and shoots. Details about how carbohydrates move to these rapidly growing organs is a mystery because the phloem is thought to be non-functional at this time of year and there is almost no xylem flow since transpiration is minimal. To address these issues, I have enlisted the help of Dr. Zwieniecki, another tree physiologist in the Plant Sciences Department and we hired a post-doctoral scientist to begin detailed studies of these phenomena. Preliminary data indicate that local storage of carbohydrates in spurs and stems is rapidly depleted during bloom and patterns of starch and soluble carbohydrate content in larger branches and the trunk are consistent with their usage by organs growing during early spring. This has led to a new hypothesis about how carbohydrates get transported to the growing organs in the spring that is being tested in Dr. Zwieniecki's laboratory.

### **Developing a Database on Standing Biomass in Almond**

Since relatively little published data are available on whole tree biomass accumulation in almond trees we have worked with a professional orchard removal company to obtain data from them on the weight of chippings they obtain subsequent to the removal of an

orchard. While this has been more difficult than anticipated, we have made good progress on this objective. Data from 61 removed orchards representing 2,034 acres indicated that orchard standing biomass varies greatly among orchards. In this set of removed orchards, the amount of dry biomass removed varied from 4 to 63 dry tons per acre, with the mean and median dry tons per acre removed being 27.7 and 26.3, respectively. Based on our orchard removal data it is likely that a standing orchard that is 20 years old or older and has a limited number of missing trees contains between 30 and 40 dry tons of biomass per acre. This would represent approximately 12 to 16 tons of carbon per acre.

In order to more accurately estimate the standing biomass of specific orchards we began ground surveying orchards to estimate orchard mean trunk cross sectional area (TCSA) prior to orchard removal and we correlated mean TCSA/acre values with standing biomass data collected upon orchard removal. While there was a good correlation between mean orchard TCSA in orchards with few missing trees, the majority of orchards being removed had substantial numbers of missing trees, or trees with highly variable sizes. Therefore, we began analyzing Google-earth images of orchards prior to their removal, to determine if aerial photography can be effectively used to provide covariate data in order to more accurately estimate standing biomass on non-uniform orchards. The results of these studies are currently being written up for publication.

### **Associated Studies**

Studies associated with this project and a previous project were based on an analysis of data from the Regional Variety trials sponsored by the Almond Board (1993-2005), data from the spur dynamics study carried out by Dr. Lampinen's laboratory from 2001 to 2007 and research of a PhD student (Katherine Pope) in Dr. DeJong's laboratory.

### **Developing an Integrated Understanding of Almond Tree Productivity**

This project and the studies associated with this project have provided a better quantitative understanding of the factors determining the productivity of almond trees. Previous research by Dr. Lampinen's laboratory (Lampinen et al. 2012) indicated that an orchard that intercepts 85% of solar radiation at mid-day should be capable of producing approximately 5000 lbs. of almond kernels. If an individual kernel weighs 1 gm, then at a standard planting density of ~120 trees per acre, each tree must produce ~19000 nuts per tree. The almond spur studies indicate that this would require ~15000 bearing spurs per tree. However, on average only ~15% of the total spur population bears fruit in any one year, so the total population of spurs in a tree is ~100,000. Of these, ~15000 spurs bear fruit in the current year, another ~15,000 bore fruit last year (our data shows that spurs very rarely bear fruit in two subsequent years), ~10% (10,000) will die (and need to be replaced), ~20% (20,000) flowered but did not bear fruit, and another ~30% (30,000) of the spurs rested in the current year potentially because they did not have enough leaf area to stimulate flower production (Lampinen et al. 2011, Tombesi et al. 2011).

The key to maintaining high yields would appear to be maintaining healthy spur populations and doing whatever is possible to stimulate increasing numbers of the

100,000 spurs to flower and set fruit in a given year. However, it should be kept in mind that if abnormally high numbers of spurs produce fruit in any one year, the percentage of spurs resting in the following year, due to previous year production will increase and the numbers of spurs in the potentially productive spur pool will decrease. It is likely that the upper limit of the number of healthy spurs that a tree can maintain is a direct function of the amount of light the tree canopy intercepts to supply adequate photosynthate to the spurs in conjunction with adequate nutrients and water available to the tree.

Our modeling studies indicate that there is an upper limit to the number of nuts that a tree can support, particularly during the period between 30 to 50 days after bloom. During this period potential fruit growth is very rapid (~1300 g/tree/day for 19,000 fruit or ~ 0.07 g/fruit/day). The estimated tree photosynthetic rate for this period is 400 – 800 g/tree/day and, thus, fruit growth is partially dependent on a dwindling supply of stored carbohydrates (the estimated total supply of available stored carbohydrates during the whole winter and spring season is ~14,000 g/tree/season) (based on Da Silva et al. 2014 and Esparza et al. 1999).

More research needs to be conducted to understand what limits the percent of spurs that produce flowers, factors that determine the percent of flowering spurs that set fruit (other than factors affecting pollination), and the rate of depletion of stored carbohydrates during the first 50 days after bloom.

### **Publications:**

Overall, this project and studies directly or indirectly associated with this project have resulted in ten significant publications related to almond tree growth and productivity.

1. The first provided an understanding of the relationship between spring temperatures and the timing of hull-split.

Fruit development in almond is influenced by early spring temperatures in California; S. Tombesi, R. Scalia, J. Connell, B. Lampinen and T.M. DeJong; *Journal of Horticultural Science and Biotechnology* (2010) 85:317-322.

Abstract: The period from full bloom (FB) to fruit maturity for individual cultivars of peach, nectarine, plum, and prune is influenced by daily temperatures between the start of FB and 30 d after FB (DAFB). Typically, warm Springs accelerate fruit development. Almond is closely-related to peach, but the date of fruit maturity is not always closely related to the date of harvest. Normally the date of “hull-split” (HS) signals the beginning of fruit maturity. The aim of this study was to determine if the length of the period between FB and HS in several important Californian almond cultivars was related to temperatures shortly after the start of FB. Data on the dates of FB and HS from three locations in the Central Valleys of California (North, Central, and South) were analyzed over 8 years to determine the effect of Spring temperatures on the duration of fruit development. Data on 28 cultivars were evaluated, but only the results for 12 of the most important cultivars are reported here. The length of the period of fruit development

from FB to HS was negatively correlated with the accumulation of degree-days between FB and 90 DAFB (mean  $R^2 = 0.51 \pm 0.3$ ), with generally poorer correlations with degree-days to 30 or 50 DAFB (mean  $R^2 = 0.31 \pm 0.02$  and  $0.36 \pm 0.3$ , respectively). These results suggest that temperatures in the first 90 DAFB are the primary factor influencing the time of nut maturity in almond cultivars in California.

Data from this paper have been used to develop a web-based model to help growers predict hull-split in their orchards by late May of each year.

See: Hull-split Prediction Model at [http://fruitsandnuts.ucdavis.edu/Weather Services/](http://fruitsandnuts.ucdavis.edu/WeatherServices/)

2. The second publication provided insight into the factors that influence individual spur productivity and mortality in almond tree canopies.

Spur behaviour in almond trees: relationships between previous year spur leaf area, fruit bearing and mortality; Bruce D. Lampinen, Sergio Tombesi, Samuel Metcalf and Theodore M. DeJong; *Tree Physiology* (2011) 31: 700-706

**Abstract:** In mature almond (*Prunus dulcis*) orchards the majority of crop is borne on spurs (short, proleptic shoots) that can live for several years and can produce from one to five fruit. Previous research has led to the hypothesis that spur longevity is related to spur light exposure, cropping and age. However, limited quantitative data are available to substantiate these hypotheses. The objective of this study was to determine spur characteristics that were most highly correlated with spur productivity and longevity in mature, bearing almond trees. We particularly focused on characteristics related to the spur light environment and spur crop load. Previous year spur leaf area was strongly related to spur viability and flowering; the greater the leaf area in the previous year, the higher the probability of spur survival into the next year and the higher the probability for the spur to bear one or more flowers. Previous year bearing also appeared to influence viability and return bloom, especially in spurs with low leaf area. These results suggest that spur source-sink balance is basic to the life cycle of almond spurs. Furthermore, the results are consistent with the hypothesis that spurs are semi-autonomous organs with respect to carbohydrate balance for much of the growing season. The models developed from this work will provide the basis for developing a functional-structural almond crop model that simulates cropping at the spur level. Finally, this information provides general thresholds for maintaining spur viability and productivity that will be useful for developing and evaluating tree training systems and orchard management practices.

3. The third publication increased understanding of the potential for almond orchards to yield large crops in two successive years.

Relationships between spur- and orchard-level fruit bearing in almond (*Prunus dulcis*); Sergio Tombesi, Bruce D. Lampinen, Samuel Metcalf and Theodore M. DeJong; *Tree Physiology* (2011) 31:1413-1421



Abstract: Almond is often considered to be a moderately alternate-bearing species but historical yield data typically do not exhibit clear patterns of alternate bearing at the orchard level, while research has indicated that spurs (the main fruit bearing unit in almond trees) rarely produce fruit in two subsequent years. The objective of the present work was to analyze the bearing behavior of almond trees at both the orchard level and the individual spur level over multiple years to explain this apparent paradox. The 10-year yield patterns of three almond cultivars grown at three different sites within California were analyzed for tendencies of alternate bearing at the orchard level. At the individual spur level, data on spur viability, and number of flowers and fruits per spur were collected on 2400 individually tagged spurs that were observed over 6 years to characterize bearing at that level. At the orchard level one cultivar (Nonpareil) did exhibit a tendency for alternate bearing at one site (Kern) but other cultivars and sites did not. The orchard and the individual trees in which the spur population study was conducted showed tendencies for alternate bearing but the spur population did not. Only a relatively small percentage of the total tagged spur population bore fruit in any given year and therefore while individual fruiting spurs exhibited a high level of non-bearing after fruiting the previous year the spurs that did produce fruit in any year generally did not constitute enough of the total spur population to exhibit alternate bearing at the whole population level. Our results suggest that annual bearing fluctuations in almond are probably mainly due to year-to-year variations of parameters affecting fruit set and that high rates of fruit set in a given year may involve a larger-than-normal percentage of a spur population in fruit bearing. This would limit the size of the spur population available for flowering in the subsequent year and could cause alternate year bearing. However, from historical records, this would appear to be the exception rather than a normal circumstance. Therefore, almond should not be considered to be a strictly alternate-bearing species.

4. A fourth study showed how spur fruiting one year leads to less spur leaf area on that spur and thus decreased subsequent year flowering and increased potential for spur mortality.

Spur fruit set is negatively related with current-year spur leaf area in almond; Sergio Tombesi, Bruce D. Lampinen, Samuel Metcalf, and Theodore M. DeJong; Hortscience (2015) 50:322–325.

Abstract: Almond spurs are known to be the primary bearing unit in almond tree and are subject to alternate bearing. Fruits are a strong sink in bearing spurs and can influence spur leaf growth. At the same time the percent of flowers that set fruit on a spur (spur relative fruit set) could be influenced by the competition among multiple flowers/fruits borne on the same spur as well as by limited leaf area on the same spur. The aim of the present work was to investigate the relationship between current-year spur leaf area and spur absolute and relative fruit set. Approximately 2400 spurs were tagged and followed over 6 years and data concerning spur leaf area, number of flowers per spur and number of fruits per spur were collected. Spur leaf area was reduced in fruiting spurs in comparison with non-fruiting spurs according to the number of fruits borne by each spur. This phenomenon contributes to spur alternate bearing because spur

flowering and survival in the next year are a function of the leaf area in the current year. Relative fruit set in almond appears to be negatively associated with current-year spur leaf area. Competition among fruits on the same spur did not appear to influence spur relative fruit set.

5. A fifth study attempted to summarize some of the practical implications of the spur dynamics project and emphasizes the importance of flower numbers compared to percent fruit set in determining yield in a well-managed orchard.

Yield in almond is related more to the abundance of flowers than the relative number of flowers that set fruit; Sergio Tombesi, Bruce D. Lampinen, Samuel Metcalf, and Theodore M. DeJong; California Agriculture (in press)

Abstract: Almond tree yield is a function of the number of flowers on a tree and the percentage of flowers that set fruit. Almond tree spur dynamics research has documented that previous year spur leaf area is a predictive parameter for year-to-year spur survival, spur flowering and to a lesser extent spur fruiting, while previous year fruit bearing has a negative impact on subsequent year flowering. However, there is still some question about whether yields are more dependent on flower numbers or relative fruit set of the flowers that are present. The aim of the present work was to determine the relative importance of flower abundance vs relative fruit set in determining the productivity of a population of tagged spurs in almond trees over a six-year period. In this study overall tree yield among years was more sensitive to spur flower density than relative fruit set. These results emphasize the importance of maintaining large populations of healthy flowering spurs for sustained high production in almond orchards.

6. This study provided statistical models for the structure of shoots of three almond cultivars that can be used in the L-almond model.

Systematic Analysis of Branching Patterns of Three Almond Cultivars with Different Tree Architectures; Negron, C., L. Contador, B. D. Lampinen, S. G. Metcalf, Y. Guedon, E. Costes and T. M. DeJong; J. Amer. Soc. Hort. Sci. (2013)138:407-415.

Abstract: Different almond (*Prunus dulcis*) cultivars have been characterized by their contrasting shoot branching patterns; however, the differences between patterns have been difficult to quantify. This study aimed to model the branching patterns of 2-year-old proleptic shoots on three almond cultivars (Nonpareil, Aldrich, and Winters) representing different tree architectures. The effects of branching pattern on flowering were also studied. The branching patterns of shoots of different length categories were assessed by a single hidden semi-Markov model for each cultivar. The models identified zones of homogeneous branching composition along shoots and were used to extract the occurrence and number of nodes of the zones according to shoot length categories. The numbers of flower buds were also determined for each shoot length category in each cultivar. The models of branching patterns of 'Nonpareil' and 'Aldrich' were similar and differed from the 'Winters' model. 'Winters' shoots produced more zones, but some of the zones had similar characteristics as previous zones and thus appeared to be repeated. This cultivar also had more spurs and syleptic shoots than the other cultivars.

The occurrence and node number of the central zones decreased along with reduction in shoot length in all the cultivars. 'Aldrich' tended to have more flower buds than comparable-length shoots of the other two cultivars. This study provides a quantitative description of the shoot branching patterns of three important cultivars and explains how branching changes in relation to shoot length, whereas production of flower buds varies despite similar branching patterns.

7. This study clarified the effects of water stress on shoot growth and will be useful in understanding long term water stress effects on almond tree growth and productivity.

*Differences in proleptic and epicormic shoot structures in relation to water deficit and growth rate in almond trees (Prunus dulcis); Negron, C, L. Contador, B. D. Lampinen, S. G. Metcalf, Y. Guedon, E. Costes and T. M. DeJong; Annals of Botany (2014)113:545-554.*

**Background and Aims** Shoot characteristics differ depending on the meristem tissue that they originate from and environmental conditions during their development. This study focused on the effects of plant water status on axillary meristem fate and flowering patterns along proleptic and epicormic shoots, as well as on shoot growth rates on 'Nonpareil' almond trees (*Prunus dulcis*). The aims were (1) to characterize the structural differences between proleptic and epicormic shoots, (2) to determine whether water deficits modify shoot structures differently depending on shoot type, and (3) to determine whether shoot structures are related to shoot growth rates.

**Methods:** A hidden semi-Markov model of the axillary meristem fate and number of flower buds per node was built for two shoot types growing on trees exposed to three plant water status treatments. The models segmented observed shoots into successive homogeneous zones, which were compared between treatments. Shoot growth rates were calculated from shoot extension measurements made during the growing season.

**Key Results:** Proleptic shoots had seven successive homogeneous zones while epicormic shoots had five zones. Shoot structures were associated with changes in growth rate over the season. Water deficit (1) affected the occurrence and lengths of the first zones of proleptic shoots, but only the occurrence of the third zone was reduced in epicormic shoots; (2) had a minor effect on zone flowering patterns and did not modify shoot or zone composition of axillary meristem fates; and (3) reduced growth rates, although patterns over the season were similar among treatments.

**Conclusions:** Two meristem types, with different latency durations, produced shoots with different growth rates and distinct structures. Differences between shoot type structure responses to water deficit appeared to reflect their ontogenetic characteristics and/or resource availability for their development. Tree water deficit appeared to stimulate a more rapid progression through ontogenetic states.

8. This study documented the influence of pruning severity on subsequent year shoot growth, structure and potential productivity.

How different pruning severities alter shoot structure: A modelling approach in young 'Nonpareil' almond trees; Claudia Negrón, Loreto Contador, Bruce D. Lampinen, Samuel G. Metcalf, Yann Guédon, Evelyne Costes and Theodore M. DeJong; *Functional Plant Biology* (2015) 42:325-335.

Abstract: Axillary meristem fate patterns along shoots, also referred to as shoot structure; appear to be fairly consistent among trees within a genotype growing under similar conditions. Less is known about shoot structural plasticity following external manipulations, such as pruning. This study on almond [*Prunus dulcis* (Mill.)] shoots aimed to answer: how pruning severity affects the structure of 1-year-old shoots that grew after pruning (regrowth shoots), the 2-year-old portion of shoots that remained from the previous year's growth after pruning (pruned shoots) and whether regrowth shoots reiterate the original structure of the 1-year-old shoots prior to pruning. Three pruning severities were imposed and the structures along the different shoots were assessed by building hidden semi-Markov models of axillary meristem fates. The structures of regrowth and pruned shoots depended on pruning severity, but maintained some of the original shoot characteristics. Regrowth shoots developed more complex structures with severe pruning, but had simpler structures than original shoots indicating progressive simplification with tree age. Pruned shoot structures were affected by the severity of pruning, by the structure when the shoots were one-year-old, and probably by local competition among buds. Changes in structure due to pruning can be modeled and be predictable.

9. Although not directly supported by this project, this study investigated relationships between bud-break based chill requirements and yield-based chill requirements of three California nut crops and indicates that almond yields are relatively insensitive to the minimal chill years experienced in California to date.

*Nut crop yield records show bud-break based chilling requirements may not reflect yield decline chill thresholds; Katherine S. Pope, Volker Dose, David Da Silva, Patrick H. Brown and Theodore M. DeJong; International Journal of Biometeorology (2015) 59:707-759*

Abstract: Warming winters due to climate change may critically affect temperate tree species. Insufficiently cold winters are thought to result in fewer viable flower buds, and the subsequent development of fewer fruits or nuts, decreasing the yield of an orchard or fecundity of a species. The best existing approximation for a threshold of sufficient cold accumulation, the "chilling requirement" of a species or variety, has been quantified by manipulating or modeling the conditions that result in dormant buds breaking. However, the physiological processes that affect bud-break are not the same as those that determine yield. This study sought to test whether bud-break based chilling thresholds can reasonably approximate the thresholds that affect yield, particularly regarding the potential impacts of climate change on temperate tree crop yields.

County-wide yield records for almond (*Prunus dulcis*), pistachio (*Pistacia vera*) and walnut (*Juglans regia*) in the Central Valley of California were compared with 50 years of weather records. Bayesian nonparametric function estimation was used to model yield potentials at varying amounts of chill accumulation. In almonds, average yields occurred when chill accumulation was close to the bud-break based chilling requirement. However, in the other two crops, pistachios and walnuts, the best previous estimate of the bud-break based chilling requirements were 19-32% higher than the chilling accumulations associated with average or above average yields. This research indicates that physiological processes beyond requirements for bud-break should to be considered when estimating chill accumulation thresholds of yield decline and potential impacts of climate change.

10. This paper presents a new approach to modeling bud-break in almond that incorporates the interaction between winter chill and heat accumulation into one model. This model should be useful for future analysis and modeling of annual cycles of almond tree growth.

A biologically based approach to modeling spring phenology in temperate deciduous trees; K.S. Pope, D. Da Silva, P.H. Brown and T.M. DeJong; Agricultural and Forest Meteorology (2014) 198:15-23.

Abstract: Prediction of the timing of spring phenological events such as bloom and leaf-out has important uses in agricultural and ecological management and modeling. However, after decades of model comparison there remains no consensus model to predict the date of spring phenological events in perennial temperate trees across species and locations. This lack of consensus may be due to over-fitting resulting from high model complexity, use of parameters that have not been adequately validated, or omission of parameters that are sound biological indicators of dormancy breaking. The aim of this study was to construct spring phenology candidate models with biologically-based parameters and starting values to test hypotheses regarding chill accumulation duration and the impact of pre-bloom conditions. Bloom data for three cultivars of *Prunus dulcis* (almond) from three decades in California were analyzed. Across all three cultivars, models which accumulated chill until approximately 75% of the heat requirement had been met, and did not integrate pre-bloom conditions, were substantially supported by the data. This suggests cold temperatures affect dormancy breaking well after the chilling requirement has been met and bud break timing is not substantially impacted by environmental conditions just prior to bud break. Fitting spring phenology using biologically based starting values estimated from bud break records may allow for the development of improved predictive models and improved approximations of critical phenological thresholds.

## Acknowledgements:

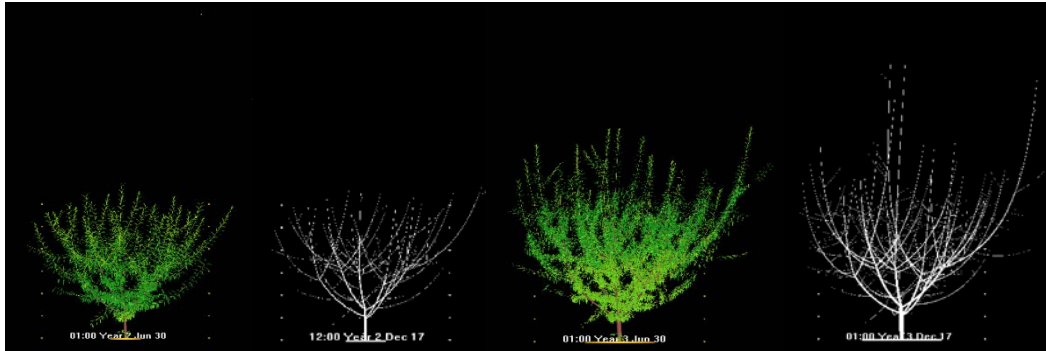
We want to formally recognize the collaboration of Drs. Evelyne Costes and Yann Guedon of UMR DAP INRA / AgroM / CIRAD / IRD Equipe Architecture et Fonctionnement des Espèces Fruitières, Montpellier, France, in helping to develop the Hidden Semi-Markov Chain models of the almond shoots. We also thank G&F Agricultural Services Inc. for their cooperation in sharing data related to orchard removals.

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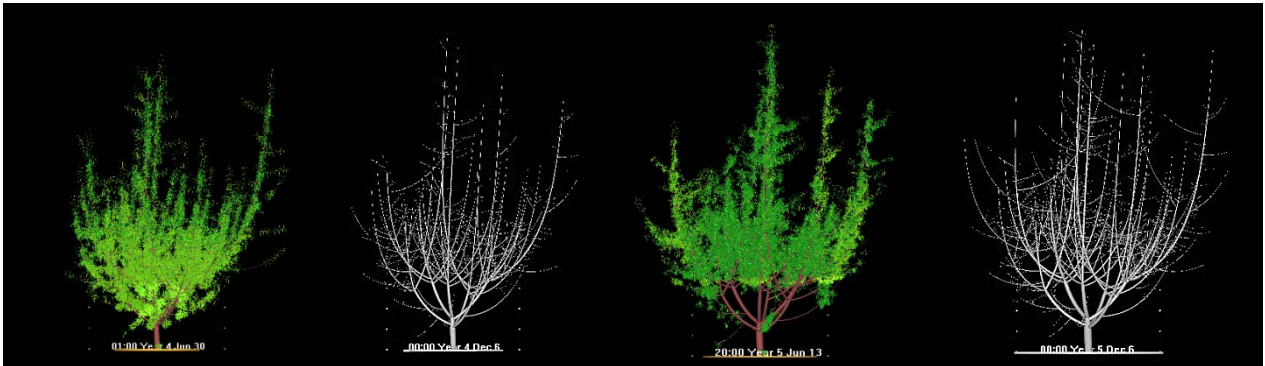
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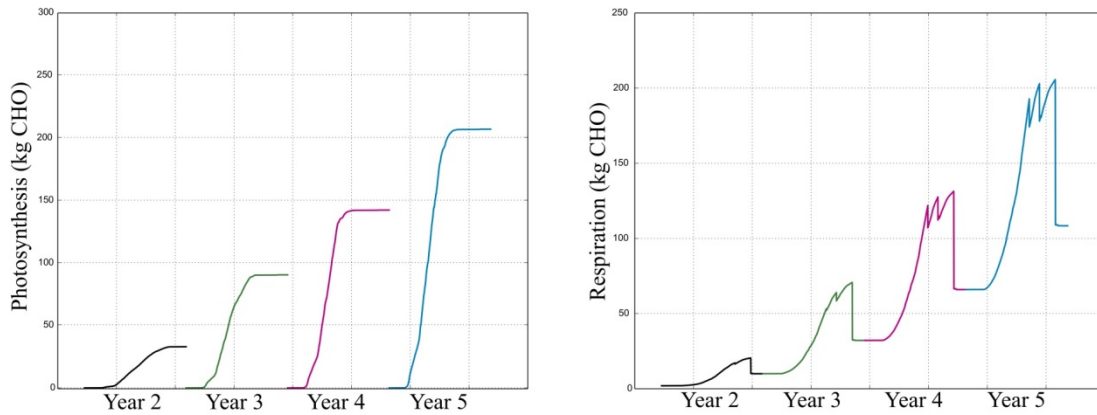
**Figures:**



**Figure 1.** Simulated almond trees in years 2 and 3 after planting in the orchard.

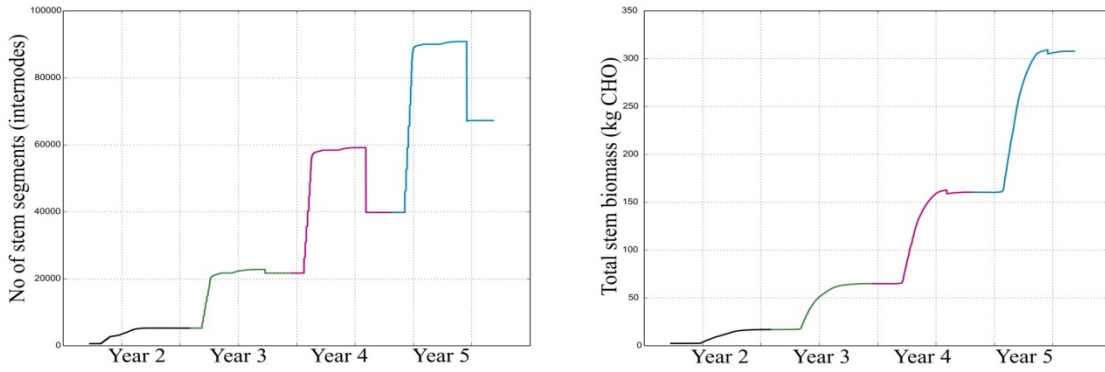


**Figure 2.** Simulated almond trees in years 4 and 5 after planting in the orchard.

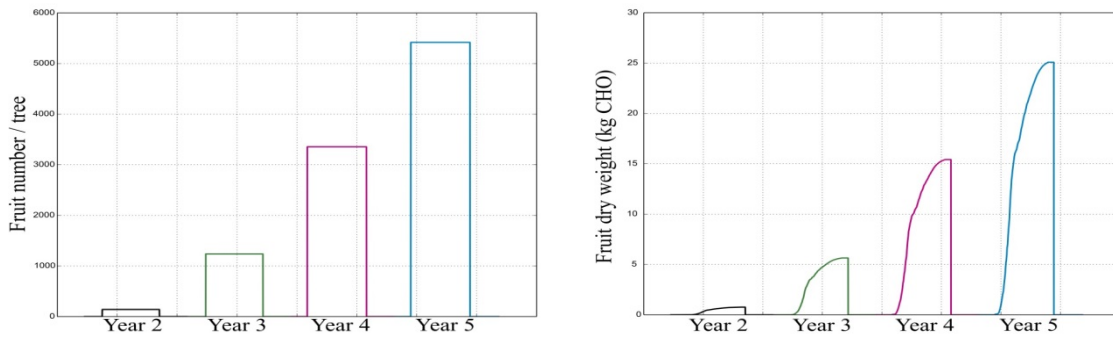


**Figure 3.** Seasonal patterns of cumulative photosynthesis and respiration for the tree parts present at specific times during years 2 to 5 of simulated growth.





**Figure 4.** The number of stem segments (internodes) and stem biomass during years 2 through 5 of simulated growth almond trees. The decrease in number of stem segments during the 4<sup>th</sup> and 5<sup>th</sup> seasons is due to the simulated effects of excess shading on stem mortality.



**Figure 5.** The number of fruit per tree and the annual accumulation of total fruit dry weight in years 2 through 5 of simulated almond tree productivity.